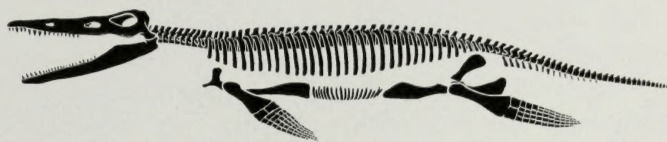


B R E V I O R A

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ECOLOGY OF THE FLAP-NECKED CHAMELEON *CHAMAELEO DILEPIS* IN SOUTHERN AFRICA

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ABSTRACT. We quantified sexual size dimorphism, reproduction, and diet in the flap-necked chameleon, *Chamaeleo dilepis*, using museum specimens. Females were larger than males in both snout-vent length (SVL) and pelvic width. The smallest sexually reproductive female was 80 mm SVL, whereas the smallest mature male was 60 mm. Female body size also correlated with clutch size (mean: 44.2, range: 19–74) and volume, suggesting the female-biased size dimorphism may be the product of fecundity selection. Males and females have slightly asynchronous reproductive cycles but breed during spring–summer. *Chamaeleo dilepis* feeds on a range of arthropods, but their diet is dominated both numerically and volumetrically by orthopterans, followed by coleopterans.

KEY WORDS: *Chamaeleo dilepis*; sexual dimorphism; reproduction; diet; flap-necked chameleon

Despite their fascinating characteristics, the life history and ecology of chameleons has been little explored, leading to a significant gap in our understanding of lizard

ecology. Chameleons have evolved a unique set of traits that allow them to occupy a highly specialized niche. Typical chameleons have telescopic eyes, fusion of some digits, a prehensile tail, and a “ballistic” tongue that can exceed the length of their body, and they are capable of rapid color change (Tilbury, 2010). These features allow chameleons to hunt with stealth and may enable them to be less conspicuous to predators during prey capture.

While the unique form and function of chameleons has attracted considerable attention, we still have only a cursory grasp of their ecology and life history, although consider-

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able work has been done on reproduction and embryonic development in *Chamaeleo calyptratus* (e.g., Andrews, 2005, 2007, 2008), and we know the female reproductive cycle for *Chamaeleo chamaeleon* (Cuadrado and Loman, 1999). We also know the foraging mode of two species from different genera. *Bradypodion pumilum* has been classified as a “cruise” forager because it spends a high enough proportion of its time moving (21%) to qualify as an active forager, but it makes very few moves per minute (Butler, 2005). Similarly, an invasive population of Jackson’s chameleon (*Chamaeleo jacksoni xanthopholis*) in Hawaii spends 19.7% of its activity time in movement, with few moves per minute ($\bar{X} = 0.24$; Hagey *et al.*, 2010). These results are surprising given the highly specialized morphological features consistent with ambush foraging and suggest that chameleons employ a foraging mode quite distinct from those of most other lizards. In terms of sexual dimorphism, the males of many species have horns or protrusions that function as either armaments or ornaments, and males can be larger than females (Necăs, 2001; Karsten *et al.*, 2009). In other species, including most of the dwarf chameleons (*Bradypodion*), females are larger than males, most likely as a result of fecundity selection (Stuart-Fox, 2009).

Here, we describe the ecology of the flap-necked chameleon, *Chamaeleo dilepis*, with particular reference to sexual dimorphism, reproduction, and diet using specimens from the Ditsong National Museum of Natural History (formerly the Transvaal Museum) in South Africa. *Chamaeleo dilepis* is a large chameleon native to savannah woodland and sometimes coastal forest in sub-Saharan Africa (FitzSimons, 1943; Brain, 1961; Pienaar, 1978; Branch, 1998; Tolley and Burger, 2007). This species is typically green or brown and usually possesses a pale stripe on the lower flanks and one to three pale patches higher on the flanks (Fig. 1; Tilbury,

2010). Interestingly, in the dry season in Kenya males tend to be brown and use defoliated vegetation, whereas females are mostly green and occupy leafy foliage. This difference falls away in the wet season when most individuals are green and occupy leafy vegetation (Hebrard and Madsen, 1984). Females are reported to be larger than males, although this has never been quantified (Brain, 1961; Necăs, 2001; Tilbury, 2010).

Chamaeleo dilepis in the wild lay their eggs in late summer in a tunnel 150–300 mm deep, excavated in damp soil. The eggs can take up to 377 days to hatch depending on environmental conditions (Brain, 1961; Wager, 1983; Branch, 1998). After egg laying, females are emaciated and generally vulnerable to a wide variety of predators that include various snakes, mongooses, raptors, hornbills, and monkeys (Pienaar, 1978; Branch, 1998; Van Wyk and Els, 2004; Cunningham and Adank, 2005; Tilbury, 2010). *Chamaeleo dilepis* has a broad distribution, and while a number of subspecies are recognized, their systematic and taxonomic status is uncertain (see Tilbury [2010] for a detailed discussion of their taxonomy). We examined only material from the southern African subregion (south and east of Kunene River separating Namibia from Angola and including southern Mozambique; see Appendix 1) and provide the first quantitative assessment of diet, reproduction and morphology.

MATERIALS AND METHODS

Dimorphism

To quantify sexual size dimorphism, we measured morphological traits from a subset of mature individuals (80 of the 251 specimens; see below for maturity criteria). Snout-vent length (SVL) was measured from the tip of the snout to the anterior edge of the cloaca



Figure 1. A typical *Chamaeleo dilepsis* from Chuka, Kenya, with characteristic pale flank patches, occipital flaps, and a row of raised triangular tubercles extending from the tip of the snout down the ventral midline. The southern African forms look identical. Photo by M. J. Whiting.

and tail length from the posterior edge of the cloaca to the tip of the tail. Head height was measured as the distance between the center of the parietal bone to the bottom of the articular. Head width was measured at the widest point of the head. Head length was measured from the tip of the snout to the back of the skull. The femur, tibia, humerus, and ulna were measured from the proximal to distal ends of the bones. Pelvic width was measured between the outer edges of the iliac bones. SVL and tail length were measured with a ruler to the nearest 1 mm, whereas digital calipers were used to measure the remaining morphological measurements to

the nearest 0.01 mm. Before testing for differences in sexual dimorphism, we removed the effect of size by regressing each morphological measurement on SVL. We made pairwise plots to determine if there were any outliers and removed one specimen from the analysis because it was an outlier in the majority of the plots. A principal components analysis was then performed on SVL and the residuals resulting from the regression of each of the measured characters on SVL. We retained the first three principal components because they explained the majority of the variation. We then used a multivariate analysis of variance (MANOVA)

on the first three principal components to determine whether trait variation among individuals of *C. dilepis* could be explained significantly by sex.

Reproduction

We made a mid-ventral incision to expose the gonads and score sexual maturity. Males were recorded as sexually mature if they contained enlarged testes and convoluted epididymides. We measured the right testis for length and width to the nearest 0.01 mm using digital calipers. Testis volume (right testis) was then determined using the formula for a prolate spheroid (Vitt *et al.*, 1993; Vitt and Zani, 2005):

$$\text{volume} = 4/3\pi(\text{length}/2) * (\text{width}/2)^2$$

We scored females as sexually mature if they contained oviductal eggs, enlarged vitellogenic follicles or a convoluted oviduct. For gravid females (sexually active), oviductal eggs were counted and the size (length and width) of each egg was measured to the nearest 0.01 mm using digital calipers. Oviductal egg volume was then calculated using the formula for a prolate spheroid (as above).

Diet

We removed stomach contents and spread them on a Petri dish for identification to order. The length and width of all intact prey items were measured to the nearest 0.01 mm using digital calipers. Prey volume was calculated using the formula for a prolate spheroid (as above).

We estimated niche breadth using the reciprocal of Simpson's (1949) diversity measure,

$$\beta = 1 / \sum_{i=1}^n P_i^2$$

where i = resource category, p = proportion of resource category i , and n = total number of categories. Values vary from 1 (exclusive use of one prey type) to n (even use of all prey types). Prey categories were the arthropod orders of prey items found in the stomach contents.

All data are reported as $\bar{X} \pm 1$ SE and differences were considered significant when alpha was < 0.05 .

RESULTS

Dimorphism

The first three principal components (PCs) explained 97% of the variation (Table 1), with PC1 explaining 79.5% of the variation, PC2 14.5%, and PC3 3.2%. PC1 loads only for body size (as represented by SVL); PC2 correlates most strongly with tail length, and to a lesser extent by head length and ulna length; and PC3 correlates primarily with tibia length, femur length, humerus length, ulna length, head height, and head length.

The sexes differ in position in the multivariate space defined by these axes (MANOVA $F_{3,75} = 3.899$, $P = 0.012$), with the first principal component being highly significant ($F_{1,75} = 7.613$, $P = 0.007$), the second component only tending toward significance ($F_{1,75} = 3.300$, $P = 0.073$), and the third being nonsignificant ($F_{1,75} = 0.783$, $P = 0.38$). Females were significantly larger than males, with the largest female measuring 162 mm SVL, whereas the largest male was only 126 mm (Table 2).

Reproduction

The smallest sexually mature female was 80 mm SVL (Fig. 2). Clutch size ($n = 25$) averaged 44.2 ± 14.7 (range, 19–74). Female SVL was significantly positively correlated with both clutch size ($r^2 = 0.472$, $F_{1,24} =$

TABLE 1. FACTOR LOADINGS OF THE FIRST THREE PRINCIPAL COMPONENTS ON SNOUT-VENT LENGTH (SVL) AND THE RESIDUALS RESULTING FROM THE REGRESSION OF EACH OF THE OTHER 13 TRAITS ON SVL MEASURED IN MALE AND FEMALE *C. DILEPSIS*. TRAITS WITH THE HIGHEST LOADINGS ARE IN ITALICS.

	Factor I	Factor II	Factor III
Snout-vent length	1.000	0	0
Head length	0	<i>0.508</i>	<i>0.673</i>
Head width	0	<i>0.275</i>	<i>0.600</i>
Head height	0	<i>0.362</i>	<i>0.698</i>
Tail length	0	<i>0.990</i>	<i>-0.139</i>
Pelvis width	0	<i>0.122</i>	<i>0.374</i>
Left ulna	0	<i>0.571</i>	<i>0.635</i>
Left humerus	0	<i>0.386</i>	<i>0.617</i>
Right ulna	0	<i>0.561</i>	<i>0.592</i>
Right humerus	0	<i>0.471</i>	<i>0.555</i>
Left tibia	0	<i>0.324</i>	<i>0.720</i>
Left femur	0	<i>0.415</i>	<i>0.610</i>
Right tibia	0	<i>0.406</i>	<i>0.726</i>
Right femur	0	<i>0.296</i>	<i>0.597</i>
Eigenvalue	353.681	64.411	14.001
Explained variance (%)	79.5	14.5	3.2

20.587, $P < 0.001$) and total egg volume ($r^2 = 0.194$, $F_{1,24} = 5.53$, $P = 0.028$), but not the largest egg measured ($r^2 = 0.015$, $F_{1,24} = 0.359$, $P = 0.55$). Seasonal variation in

ovarian volume of the largest follicle showed that females start to produce eggs in November, tapering off in May. A single female contained a clutch of developed eggs in August (Fig. 3A).

The smallest sexually mature male measured 60 mm SVL (Fig. 2). Log testicular volume increased with log SVL ($r^2 = 0.349$, $F_{1,107} = 57.361$, $P < 0.001$). Testicular volume was largest from September to February (spring and summer), with a few males showing enlarged testes in May, June, and July (Fig. 3B).

Diet

We identified 13 prey categories in the stomachs of 206 *C. dilepsis* (the remaining 45 were empty; Table 3, Fig. 4A, B). Although the majority of prey items consumed were arthropods, a snail and two reptiles (a skink and a gecko) were found in three individuals (Fig. 4A). Most of the arthropods consumed were insects (85.4%). Orthopterans dominated the diet, making up 36.4% numerically (Fig. 4A) and 68.9% volumetrically (Fig. 4B), as well as being consumed by most chameleons (37.5%). Coleopterans were also an

TABLE 2. SUMMARY OF SEXUAL SIZE DIMORPHISM IN 14 MORPHOLOGICAL TRAITS IN FEMALE AND MALE *C. DILEPIS*.

Trait (mm)	Adult Females (n = 41)		Adult Males (n = 39)	
	$\bar{X} \pm SE$	Range	$\bar{X} \pm SE$	Range
Snout-vent length	91.27 \pm 3.07	50.00–140.00	87.23 \pm 3.10	58.00–142.00
Tail length	87.59 \pm 3.20	48.00–141.00	86.03 \pm 3.00	57.00–141.00
Head height	20.72 \pm 0.69	11.83–32.06	19.74 \pm 0.60	14.37–29.18
Head width	15.47 \pm 0.59	9.04–23.26	14.67 \pm 0.51	10.10–22.26
Head length	29.10 \pm 0.89	17.63–42.89	28.38 \pm 0.92	20.44–43.58
Right femur	21.92 \pm 0.83	10.98–36.84	20.32 \pm 0.73	13.65–34.98
Right tibia	18.48 \pm 0.72	9.08–28.26	17.10 \pm 0.60	10.52–27.89
Left femur	21.39 \pm 0.82	10.54–35.50	20.04 \pm 0.73	13.28–32.34
Left tibia	18.40 \pm 0.72	9.26–28.75	17.24 \pm 0.57	11.48–27.00
Right humerus	19.03 \pm 0.65	9.87–28.21	18.31 \pm 0.62	11.70–28.32
Right ulna	18.16 \pm 0.64	9.94–27.77	17.52 \pm 0.62	11.51–28.62
Left humerus	19.13 \pm 0.66	10.87–28.01	18.56 \pm 0.66	12.16–30.24
Left ulna	18.32 \pm 0.64	9.61–28.11	17.58 \pm 0.65	11.26–29.87
Pelvis width	7.97 \pm 0.29	4.08–10.78	7.19 \pm 0.27	4.78–11.41

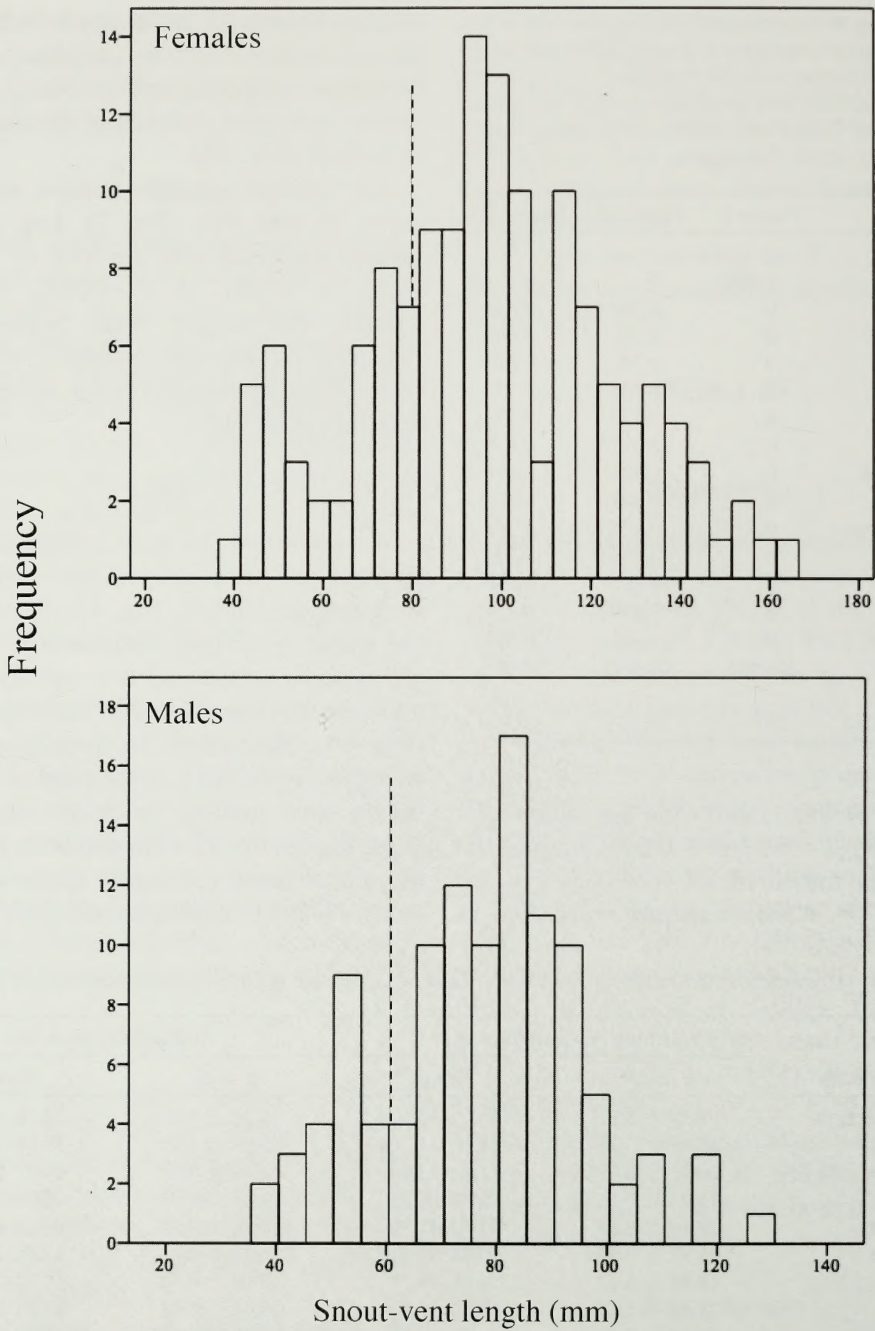


Figure 2. Frequency distribution of SVL of female and male *Chamaeleo dilepis* examined in this study. Dashed lines represent the smallest SVL at sexual maturity. See Table 2 for $\bar{X} \pm SE$ of all morphological traits measured.

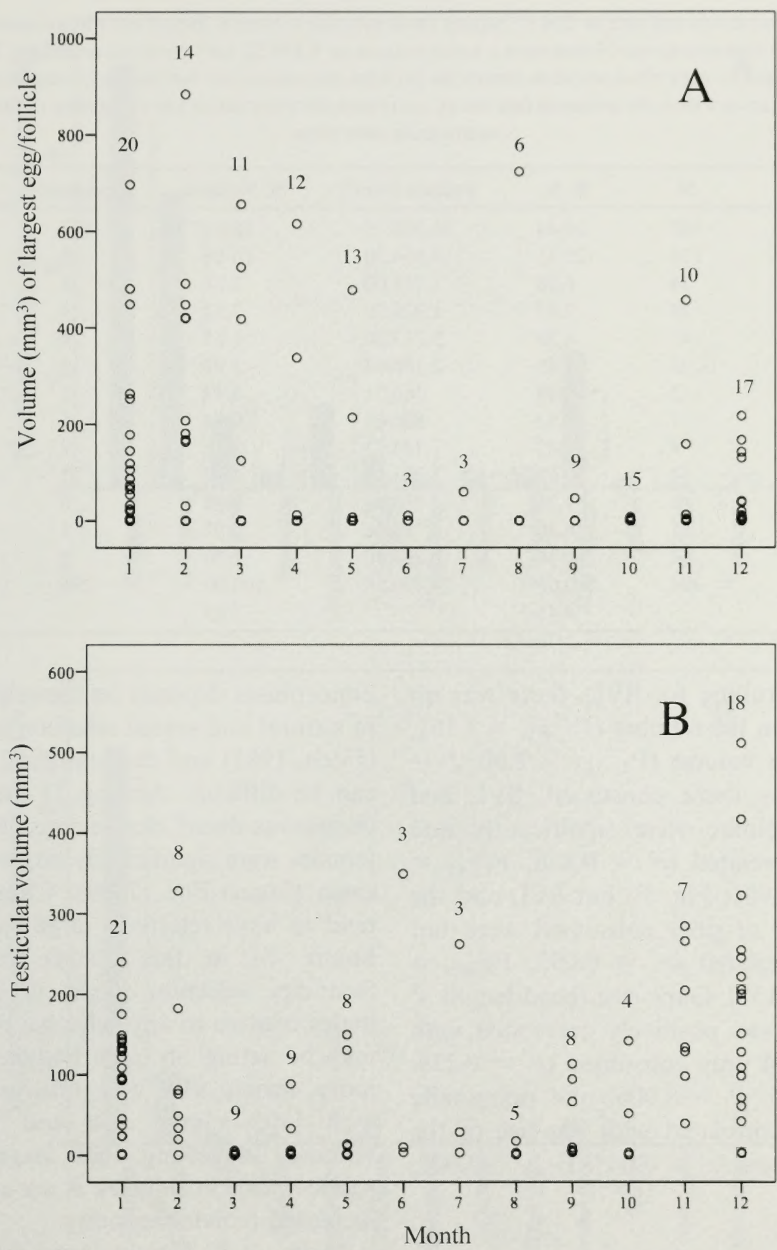


Figure 3. Egg/follicle volume (A) and testicular volume (of right testes) (B) in relation to the time of year.

important prey item, making up 25.5% of the diet numerically and 10.6% volumetrically. After orthopterans, coleopterans were also consumed by the most individual chameleons (25.3%). Niche breadths of proportion prey

number and prey volume indicate that although prey items made up similar components of *C. dilepsis*' diet numerically, prey volume was dominated by orthopterans (Table 3).

TABLE 3. COMPOSITION OF THE DIET OF 206 *C. DILEPIS* FROM SOUTHERN AFRICA. INSECT PREY WERE IDENTIFIED TO ORDER. WE EXCLUDED 59 UNIDENTIFIED PREY ITEMS WITH A TOTAL VOLUME OF 4,899.32 MM³ FROM THE SUMMARY. DIET IS REPORTED AS THE TOTAL NUMBER OF PREY ITEMS FOUND IN STOMACHS (N) WITH THE ASSOCIATED PERCENTAGE; VOLUME WAS CALCULATED USING THE FORMULA FOR A PROLATE SPHEROID (SEE TEXT), AND FREQUENCY REFERS TO THE NUMBER OF LIZARDS CONTAINING A PARTICULAR PREY ITEM.

Prey Type	N	% N	Volume (mm ³)	% Volume	Frequency	% Frequency
Orthoptera	180	36.44	51,308.75	68.91	111	37.50
Coleoptera	126	25.51	7,864.30	10.56	75	25.34
Diptera	34	6.88	1,718.00	2.31	18	6.08
Mantodea	10	2.02	1,729.70	2.32	9	3.04
Hymenoptera	41	8.30	1,213.20	1.63	24	8.11
Hemiptera	22	4.45	2,166.64	2.91	12	4.05
Phasmatodea	2	0.40	366.71	0.49	2	0.68
Odonata	7	1.42	626.63	0.84	6	1.74
Diplopoda	9	1.82	1,744.73	2.34	9	3.04
Larvae/pupa	54	10.93	3,703.43	4.97	21	7.09
Spiders	6	1.21	736.02	0.99	6	2.03
Mollusks	1	0.20	14.06	0.02	1	0.34
Vertebrates	2	0.40	1,264.40	1.70	2	0.68
Totals	494	100.00	74,456.58	100.00	296	100.00
Niche breadths		4.45		2.03		

When controlling for SVL, there was no effect of sex on the number ($F_{1, 205} = 3.161$, $P = 0.077$) or volume ($F_{1, 145} = 2.00$, $P = 0.159$) of prey items consumed. SVL and total prey volume were significantly and positively correlated ($r^2 = 0.456$, $F_{1,145} = 2.667$, $P < 0.001$; Fig. 5), but SVL and the total number of prey consumed were not significantly related ($r^2 = 0.092$, $F_{1,205} = 1.242$, $P = 0.137$). Gape size (head length \times head width) was positively correlated with the number of prey consumed ($r^2 = 0.114$, $F_{1,64} = 8.115$, $P = 0.006$) and marginally significantly correlated with the size of the largest prey item ($r^2 = 0.083$, $F_{1,45} = 4.008$, $P = 0.051$).

DISCUSSION

Of the 14 morphological variables we measured in *C. dilepis*, only SVL and pelvic width differed significantly between the sexes. Females were significantly larger than males in both SVL and pelvic width. In squamate reptiles, the degree of sexual

dimorphism depends on the relative strength of natural and sexual selection on both sexes (Fitch, 1981) and disentangling these effects can be difficult. Among 21 lineages of the viviparous dwarf chameleons (*Bradypodion*), females were significantly larger in 15 (71%) cases (Stuart-Fox, 2009). Chameleons also tend to have relatively large clutches (maximum, 74 in this study) and as such, fecundity selection might favor larger females relative to any selective pressures that may be acting on male body size. Furthermore, female SVL was positively correlated with both clutch size and total clutch volume, suggesting that larger SVL and pelvic width in females is an adaptation to increased female fecundity.

Male and female reproductive cycles did not appear to be highly synchronized. Females appear to be seasonal, commencing vitellogenesis in summer (November) and containing fully developed eggs throughout the warmer months of the year (November–May). Males have winter and summer peaks in testes volume and appear to commence

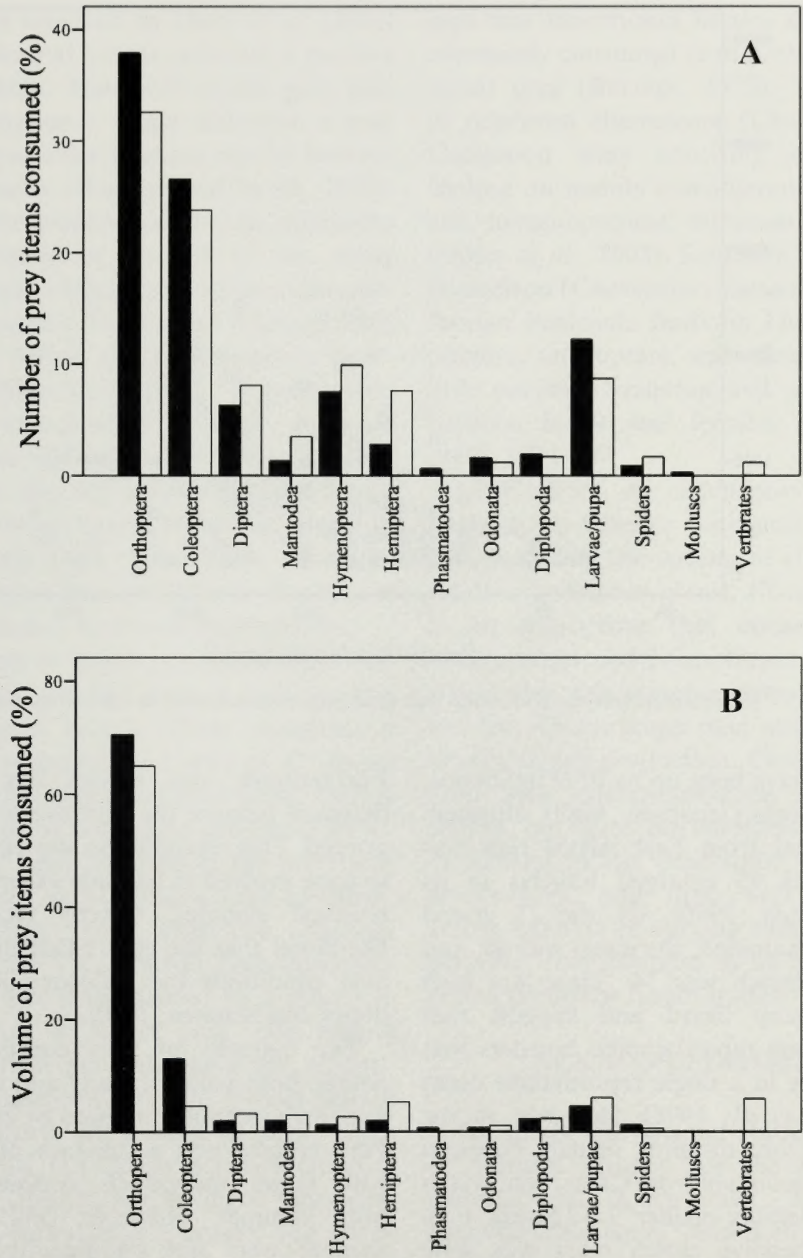


Figure 4. Comparison of the diet of female (dark bars) and male (clear bars) *Chamaeleo dilepis*. Prey number (A) and volume (B) are presented as percentages.

spermatogenesis one to two months earlier in spring (September). Although we were not able to determine if individual females lay multiple clutches in a season, the temporal

distribution of fully developed eggs raises this possibility. Female *C. dilepis* invest heavily in reproduction by producing large clutches of small eggs. Previous reports of

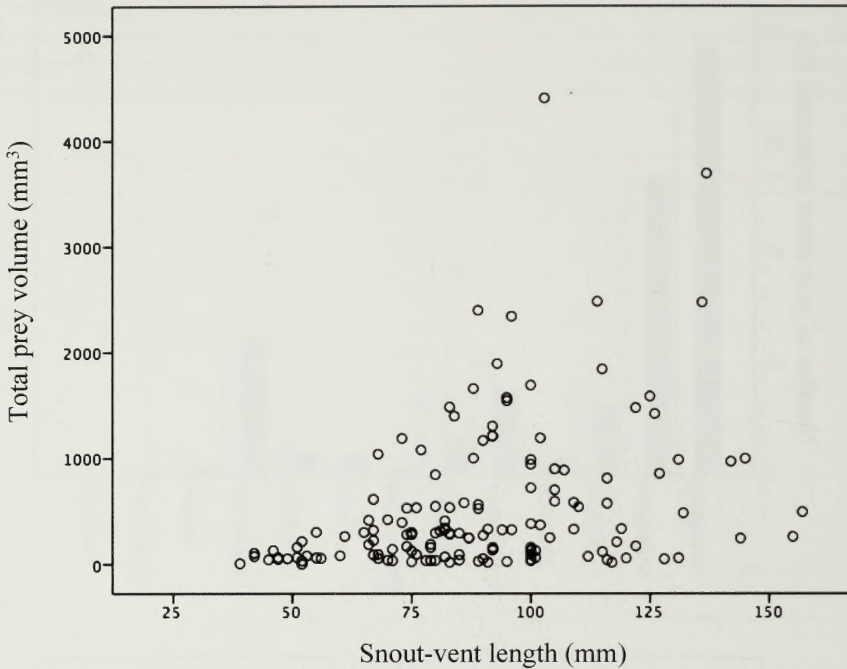


Figure 5. Relationship between SVL (mm) and total prey volume (mm^3) in *Chamaeleo dilepsis*.

clutch sizes have been up to 50 (FitzSimons, 1943) or 77 eggs (Jacobsen, 1989), although one individual from East Africa that was dissected had 95 enlarged follicles in its oviducts (Fitch, 1970). Of the 25 gravid females we examined, the mean was 44, and the largest clutch was 74. These are high values for any lizard and suggest that chameleons are typical capital breeders that invest heavily in a single reproductive event (see Bonnet *et al.*, 1998). However, in the similar sized but distantly related *Trioceros* [*Chamaeleo*] *montium* from Cameroon, clutch size is considerably smaller: 3–12 (mean, 6.5), and mean relative clutch mass was 40% (Herrmann and Herrmann, 2005). Andrews and Karsten (2010) provide an excellent review of the evolution of reproductive mode, developmental rate, and body size in chameleons. In the context of their review, *C. dilepsis* is a relatively large sized, derived chameleon that develops comparatively slowly.

Furthermore, this species has embryonic diapause because the eggs overwinter underground. This reproductive strategy is thought to have evolved in habitats experiencing dry, seasonal climates, thereby increasing the likelihood that the eggs hatch during favorable conditions the following season (Andrews and Karsten, 2010).

The majority of prey consumed by *C. dilepsis*, both volumetrically and numerically, were orthopterans, followed by coleopterans. Prey volume was a function of body size, with larger individuals consuming larger prey volumes. However, SVL and prey number were not significantly correlated, possibly because most individuals contained relatively few prey items. Gape size was correlated with both prey number and the largest prey item consumed. A relatively large number of individuals contained prey items in their stomach (82%), suggesting that *C. dilepsis* feed frequently. This agrees with

the patterns reported by Huey *et al.* (2001) that most diurnal lizards maintain a positive energy balance. Nine individuals were also found to contain a single millipede, a prey item usually avoided by many reptiles because of their toxicity (Wapstra and Swain, 1996). However, the presence of noxious millipedes has been found in the diet of two other African species (African tree agama, *Acanthocercus a. atricollis*, Reaney and Whiting, 2002; Wahlberg's velvet gecko, *Homopholis wahlbergii*, Whiting *et al.*, 2007). Together with numerous anecdotal reports of millipede consumption (Branch, 1998), these studies suggest that they are at least occasional prey items of African lizards either because they are less toxic than their North American counterparts or because African lizards are better adapted to deal with their toxicity.

In addition to insects, six chameleons had eaten spiders, one had eaten a mollusk, and two had eaten lizards. These constitute a very small proportion ($< 4\%$) of *C. dilepis* specimens that contained food items. Only a few instances of vertebrate predation by *C. dilepis* have been reported in the literature, including two geckos and a case of cannibalism (Tilbury, 2010). Therefore, although *C. dilepis* may on occasion take noninsect prey, their diet is dominated by a relatively narrow range of insect prey. Our results largely confirm previous anecdotal reports. *Chamaeleo dilepis* is reported to feed mainly on grasshoppers and beetles (Branch, 1998; Tilbury, 2010), but also to include occasional butterflies, dragonflies, winged termites, myriapods, various flying insects, and invertebrates such as snails and spiders (Fitz-Simons, 1943; Brain, 1961; Pienaar, 1978). The similarly sized *Chamaeleo namaquensis*, which is terrestrial, has a similar diet, ex-

cept that tenebrionid beetles are their most commonly consumed (and probably encountered) prey (Burrage, 1973). Three species of rainforest chameleons (*Chamaeleo*) from Cameroon were relatively opportunistic, feeding on mainly coleopterans, heteropterans, hymenopterans, dipterans, and spiders (Hofer *et al.*, 2003). Similarly, the common chameleon (*Chamaeleo chamaeleon*) from the Iberian Peninsula feeds on Diptera, Hymenoptera, Orthoptera, and Heteroptera with little seasonal variation and no differences between males and females (Pleguezuelos *et al.*, 1999).

In summary, our study provides the first quantitative baseline ecological data for *C. dilepis*, one of few species of chameleons to occur in a savanna biome. *Chamaeleo dilepis* is an insectivore that consumes mostly orthopterans and coleopterans; they follow a typical spring–summer reproductive cycle, and females are larger than males and invest heavily in egg production. Chameleons have long been underrepresented in ecological studies, but given the substantial investment of females in egg production, their unique morphology, and their wide distribution across habitats of varying rainfall and temperature, they promise to be an interesting model group for future studies.

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APPENDIX 1. SPECIMENS EXAMINED FROM THE DITSONG NATIONAL MUSEUM OF NATURAL HISTORY.

Catalog No.	Location (quarter degree grid square)	Country
14469	2027Cc	BOTSWANA
14473	Gabarone	BOTSWANA
30655	1922Ca	BOTSWANA
30656	1922Ca	BOTSWANA
30657	1922Ca	BOTSWANA
30863	1921Ca	BOTSWANA
31099	1821Bd	BOTSWANA
45699	1923Cb	BOTSWANA
14470	1923Cd	BOTSWANA
14471	1923Cd	BOTSWANA
14472	Makgadikagi	BOTSWANA
26965	Kube pan	BOTSWANA
30633	Nokaneng	BOTSWANA
30658	1922Ca	BOTSWANA
30659	1922Ca	BOTSWANA
31094	1821Ba	BOTSWANA
41463	Botswana	BOTSWANA
2471	2555S 3230E	MOZAMBIQUE
3934	2532Ba	MOZAMBIQUE
29258	2233Dc	MOZAMBIQUE
29325	2233Dc	MOZAMBIQUE
29371	2433Cd	MOZAMBIQUE
29372	2433Cd	MOZAMBIQUE
29375	2433Cd	MOZAMBIQUE
29380	2433Cd	MOZAMBIQUE
29401	2233Cd	MOZAMBIQUE
80934	1659S 3843E	MOZAMBIQUE
80968	1703S 3844E	MOZAMBIQUE
80969	1703S 3844E	MOZAMBIQUE
29156	2600S 3255E	MOZAMBIQUE
29314	2233Cd	MOZAMBIQUE
29377	2433Cd	MOZAMBIQUE
17063	1724S 1553E	NAMIBIA
17065	1724S 1553E	NAMIBIA
23988	2015Ab	NAMIBIA
25090	1920Da	NAMIBIA
31193	2311S 1629E	NAMIBIA
36359	2308S 1628E	NAMIBIA
39187	1724Ad	NAMIBIA
39207	1724Ad	NAMIBIA
39354	1724Ad	NAMIBIA
40061	1816Dd	NAMIBIA
52784	1914Dd	NAMIBIA
17066	1724S 1553E	NAMIBIA
22618	1724Ad	NAMIBIA
43710	1724Cb	NAMIBIA
57411	1920Dd	NAMIBIA
68751	1952S 1354E	NAMIBIA
118	2506S 3027E	SOUTH AFRICA

APPENDIX 1. CONTINUED.

Catalog No.	Location (quarter degree grid square)	Country
1263	2329CD	SOUTH AFRICA
2663	TVL	SOUTH AFRICA
4570	2328CB	SOUTH AFRICA
7386	2330DC	SOUTH AFRICA
7387	2330DC	SOUTH AFRICA
9479	TVL	SOUTH AFRICA
11053	2328CB	SOUTH AFRICA
11635	2435S 3104E	SOUTH AFRICA
13926	TVL	SOUTH AFRICA
14216	TVL	SOUTH AFRICA
14219	TVL	SOUTH AFRICA
24722	TVL	SOUTH AFRICA
26062	2528CA	SOUTH AFRICA
26079	2528CA	SOUTH AFRICA
43973	2428CB	SOUTH AFRICA
45757	2229DC	SOUTH AFRICA
47430	2528CB	SOUTH AFRICA
50679	2529AC	SOUTH AFRICA
52149	2528CB	SOUTH AFRICA
52533	2526CB	SOUTH AFRICA
61772	2627CD	SOUTH AFRICA
61775	2428CC	SOUTH AFRICA
61777	2330AB	SOUTH AFRICA
61779	2230DA	SOUTH AFRICA
61780	2429BB	SOUTH AFRICA
61781	2328DB	SOUTH AFRICA
61793	2328CD	SOUTH AFRICA
61794	2431CA	SOUTH AFRICA
61799	2528CA	SOUTH AFRICA
61800	2529CC	SOUTH AFRICA
61801	2627CB	SOUTH AFRICA
61802	2230DA	SOUTH AFRICA
61804	2330DB	SOUTH AFRICA
61805	2229DA	SOUTH AFRICA
61806	TVL	SOUTH AFRICA
61807	2430DA	SOUTH AFRICA
67621	2438S 3128E	SOUTH AFRICA
82096	2528AD	SOUTH AFRICA
61797A	2528BA	SOUTH AFRICA
61797B	2230DA	SOUTH AFRICA
1214	2330AA	SOUTH AFRICA
1215	2330AA	SOUTH AFRICA
1216	2330AA	SOUTH AFRICA
1388	TVL	SOUTH AFRICA
1901	2345S 3015E	SOUTH AFRICA
1985	2528CA	SOUTH AFRICA
26053	2506S 3027E	SOUTH AFRICA
28872	KNP	SOUTH AFRICA
30211	2330CD	SOUTH AFRICA

APPENDIX 1. CONTINUED.

Catalog No.	Location (quarter degree grid square)	Country
33554	2329DD	SOUTH AFRICA
35669	2330AB	SOUTH AFRICA
47855	2628AA	SOUTH AFRICA
50230	2431DD	SOUTH AFRICA
61774	2427BA	SOUTH AFRICA
61776	2427BB	SOUTH AFRICA
61778	2428CD	SOUTH AFRICA
61782	2627CA	SOUTH AFRICA
61783	2230AC	SOUTH AFRICA
61784	2527CB	SOUTH AFRICA
61785	2630DD	SOUTH AFRICA
61786	2528BC	SOUTH AFRICA
61787	2329DB	SOUTH AFRICA
61789	2526CB	SOUTH AFRICA
61791	2426DC	SOUTH AFRICA
61792	2431CB	SOUTH AFRICA
61795	2528BD	SOUTH AFRICA
61796	2329CA	SOUTH AFRICA
80135	2627AD	SOUTH AFRICA
80	2329Cd	SOUTH AFRICA
119	2506S 3027E	SOUTH AFRICA
132	2017Ad	SOUTH AFRICA
133	2017Ad	SOUTH AFRICA
140	2430Ba	SOUTH AFRICA
149	2528Ca	SOUTH AFRICA
643	TVL	SOUTH AFRICA
719	2531Cc	SOUTH AFRICA
720	Barberton	SOUTH AFRICA
721	Barberton	SOUTH AFRICA
1080	2528Ca	SOUTH AFRICA
1134	2627Ba	SOUTH AFRICA
1199	2528Ca	SOUTH AFRICA
1254	2527Dc	SOUTH AFRICA
1264	2329Cd	SOUTH AFRICA
1702	2528S 3058E	SOUTH AFRICA
2035	2528Ca	SOUTH AFRICA
2061	Pietersburg	SOUTH AFRICA
2364	Vygeboomspt	SOUTH AFRICA
2486	2628Aa	SOUTH AFRICA
2717	2550S 2813E	SOUTH AFRICA
3373	2530Dc	SOUTH AFRICA
3374	2530Dc	SOUTH AFRICA
3975	2528Ca	SOUTH AFRICA
4500	Barberton	SOUTH AFRICA
11056	2429Aa	SOUTH AFRICA
13023	2409S 3015E	SOUTH AFRICA
13267	2546S 2814E	SOUTH AFRICA
13296	Zeerust	SOUTH AFRICA
13563	Pietersburg	SOUTH AFRICA

APPENDIX 1. CONTINUED.

Catalog No.	Location (quarter degree grid square)	Country
14366	Vaal Dam	SOUTH AFRICA
31144	2254S 2931E	SOUTH AFRICA
33261	2523Ca	SOUTH AFRICA
34616	2453S 2817E	SOUTH AFRICA
34617	2453S 2817E	SOUTH AFRICA
64331	2508S 2840E	SOUTH AFRICA
81	2329Cd	SOUTH AFRICA
120	2506S 3027E	SOUTH AFRICA
121	2506S 3027E	SOUTH AFRICA
134	2017Ad	SOUTH AFRICA
142	2430Ba	SOUTH AFRICA
148	2528Ca	SOUTH AFRICA
165	2528Ca	SOUTH AFRICA
670	2531Cc	SOUTH AFRICA
1132	2528Ca	SOUTH AFRICA
1899	2329Dd	SOUTH AFRICA
1948	2528Ca	SOUTH AFRICA
2047	2527Cc	SOUTH AFRICA
2048	2527Ca	SOUTH AFRICA
2060	2329Cd	SOUTH AFRICA
2062	2329Cd	SOUTH AFRICA
2365	2446S 2826E	SOUTH AFRICA
2488	2628Aa	SOUTH AFRICA
2489	2628Aa	SOUTH AFRICA
2540	Leysdorp	SOUTH AFRICA
3577	2329Cd	SOUTH AFRICA
3767	2428Ad	SOUTH AFRICA
3956	Modderack	SOUTH AFRICA
3976	2528Ca	SOUTH AFRICA
4279	Nylstroom	SOUTH AFRICA
4451	Koster	SOUTH AFRICA
4501	Barberton	SOUTH AFRICA
4730	Nylstroom	SOUTH AFRICA
12509	2435S 3104E	SOUTH AFRICA
13561	2329Cd	SOUTH AFRICA
14215	Tshakoma	SOUTH AFRICA
14367	Hope	SOUTH AFRICA
33824	2453S 2817E	SOUTH AFRICA
33895	2453S 2817E	SOUTH AFRICA
57314	2536S 2824E	SOUTH AFRICA
64243	2349S 3003E	SOUTH AFRICA
65728	2442S 3131E	SOUTH AFRICA
65935	2532S 3059E	SOUTH AFRICA
66166	2306S 2902E	SOUTH AFRICA
66167	2306S 2902E	SOUTH AFRICA
67273	2438S 3128E	SOUTH AFRICA
67470	2502S 3113E	SOUTH AFRICA
67619	2438S 3128E	SOUTH AFRICA
13769	Mahaba	SOUTH AFRICA

APPENDIX 1. CONTINUED.

Catalog No.	Location (quarter degree grid square)	Country
13777	Mangusi	SOUTH AFRICA
13778	Mangusi	SOUTH AFRICA
14075	2812S 3228E	SOUTH AFRICA
37993	Sodwana	SOUTH AFRICA
45715	2732Ba	SOUTH AFRICA
45733	2732Bc	SOUTH AFRICA
46026	2732BC	SOUTH AFRICA
47941	2732Bd	SOUTH AFRICA
48272	2732Bc	SOUTH AFRICA
50728	2731Cb	SOUTH AFRICA
51689	2930Cb	SOUTH AFRICA
51706	3030Bc	SOUTH AFRICA
55148	3058S 3017E	SOUTH AFRICA
56484	2930Dd	SOUTH AFRICA
65231	3043S 3010E	SOUTH AFRICA
65260	2850S 2959E	SOUTH AFRICA
66577	2832Ad	SOUTH AFRICA
66578	2832Ad	SOUTH AFRICA
66579	2832Ad	SOUTH AFRICA
66581	2832Ad	SOUTH AFRICA
67221	2832Ad	SOUTH AFRICA
68048	2826S 3231E	SOUTH AFRICA
69051	2832Ad	SOUTH AFRICA
79356	3030Cd	SOUTH AFRICA
13779		SOUTH AFRICA
30221	Illovo Beach	SOUTH AFRICA
51707	3030Bc	SOUTH AFRICA
52372	2831Cd	SOUTH AFRICA
54579	2852S 3222E	SOUTH AFRICA
55154	2930S 3014E	SOUTH AFRICA
57528	3030Cb	SOUTH AFRICA
62756	2832Ba	SOUTH AFRICA
62859	2832Ad	SOUTH AFRICA
62866	2832Ad	SOUTH AFRICA
64175	2823S 3225E	SOUTH AFRICA
66576	2832Ad	SOUTH AFRICA
66580	2832Ad	SOUTH AFRICA
67185	2832Ab	SOUTH AFRICA
67307	2904S 2904E	SOUTH AFRICA
67369	2847S 3205E	SOUTH AFRICA
67583	2827S 3226E	SOUTH AFRICA
71881	2743S 2955E	SOUTH AFRICA
82099	2832Dc	SOUTH AFRICA
16202	2032Bc	ZIMBABWE
16204	2032Bc	ZIMBABWE
18555	2032Ab	ZIMBABWE
18729		ZIMBABWE
22398	1832Bd	ZIMBABWE
34459		ZIMBABWE

APPENDIX 1. CONTINUED.

Catalog No.	Location (quarter degree grid square)	Country
55112	Kariba area	ZIMBABWE
83516	Mbalabala	ZIMBABWE
18558	2032Bc	ZIMBABWE
18559	2032Bc	ZIMBABWE
21581	1730Cb	ZIMBABWE
45962	1826Dd	ZIMBABWE

LITERATURE CITED

- ANDREWS, R. M. 2005. Incubation temperature and sex ratio of the veiled chameleon (*Chamaeleo calyptratus*). *Journal of Herpetology* 39: 515–518.
- ANDREWS, R. M. 2007. Effects of temperature on embryonic development of the veiled chameleon, *Chamaeleo calyptratus*. *Comparative Biochemistry and Physiology* 148A: 698–706.
- ANDREWS, R. M. 2008. Effects of incubation temperature on growth and performance of the veiled chameleon (*Chamaeleo calyptratus*). *Journal of Experimental Zoology* 309A: 435–446.
- ANDREWS, R. M., AND K. B. KARSTEN. 2010. Evolutionary innovations of squamate reproductive and developmental biology in the family Chamaeleonidae. *Biological Journal of the Linnean Society* 100: 656–668.
- BONNET, X., D. BRADSHAW, AND R. SHINE. 1998. Capital versus income breeding: an ectothermic perspective. *Oikos* 83: 333–342.
- BRAIN, C. K. 1961. *Chamaeleo dilepis*—a study on its biology and behaviour. *Journal of the Herpetological Association of Rhodesia* 15: 15–20.
- BRANCH, B. 1998. *Field Guide to Snakes and Other Reptiles of Southern Africa*. 3rd ed. Cape Town, Struik Publishers.
- BURRAGE, B. R. 1973. Comparative ecology and behavior of *Chamaeleo pumilus pumilus* (Gmelin) & *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). *Annals of the South African Museum* 61.
- BUTLER, M. A. 2005. Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm? *Biological Journal of the Linnean Society* 84: 797–808.
- CUADRADO, M., AND J. LOMAN. 1999. The effects of age and size on reproductive timing in female *Chamaeleo chamaeleon*. *Journal of Herpetology* 33: 6–11.
- CUNNINGHAM, P. L., AND W. ADANK. 2005. Chamaeleonidae: *Chamaeleo dilepis* Leach, 1819: flap-necked chameleon prey. *African Herp News* 38: 19–20.
- FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. *University of Kansas Museum of Natural History Miscellaneous Publication* 52.
- FITCH, H. S. 1981. Sexual size differences in reptiles. *University of Kansas Museum of Natural History Miscellaneous Publication* 70.
- FITZSIMONS, V. F. 1943. The lizards of South Africa. *Transvaal Museum Memoir No. 1*.
- HAGEY, T. J., J. B. LOSOS, AND L. J. HARMON. 2010. Cruise foraging of invasive chameleons (*Chamaeleo jacksonii xantholophus*) in Hawai'i. *Breviora* 519: 1–7.
- HEBRARD, J. J., AND T. MADSEN. 1984. Dry season intersexual habitat partitioning by flap-necked chameleons (*Chamaeleo dilepis*) in Kenya. *Biotropica* 16: 69–72.
- HERRMANN, P. A., AND H.-W. HERRMANN. 2005. Egg and clutch characteristics of the mountain chameleon, *Chamaeleo montium*, in southwestern Cameroon. *Journal of Herpetology* 39: 154–157.
- HOFER, U., H. BAUR, AND L.-F. BERSIER. 2003. Ecology of three sympatric species of the genus *Chamaeleo* in a tropical upland forest in Cameroon. *Journal of Herpetology* 37: 203–207.
- HUEY, R. B., E. R. PIANKA, AND L. J. VITT. 2001. How often do lizards “run on empty”? *Ecology* 82: 1–7.
- JACOBSEN, N. H. G. 1989. A herpetological survey of the Transvaal. Unpubl. Ph.D. Dissertation. University of Natal, South Africa.
- KARSTEN, K. B., L. N. ANDRIAMANDIMBIARISOA, S. F. FOX, AND C. J. RAXWORTHY. 2009. Sexual selection on body size and secondary sexual characters in 2 closely related, sympatric chameleons in Madagascar. *Behavioral Ecology* 20: 1079–1088.
- NECÁS, P. 2001. *Chameleons: Nature's Hidden Jewels*. Malabar, Florida, Krieger Publishing.
- PIENAAR, U. DE V. 1978. *The Reptile Fauna of the Kruger National Park*. Pretoria, Sigma Press.
- PLEGUEZUELOS, J. M., J. C. POVEDA, R. MONTERRUBIO, AND D. ONTIVEROS. 1999. Feeding habits of the common chameleon *Chamaeleo chamaeleon* (Linnaeus, 1758) in the southeastern Iberian Peninsula. *Israel Journal of Zoology* 45: 267–276.

- REANEY, L. T., AND M. J. WHITING. 2002. Life on a limb: ecology of the tree agama (*Acanthocercus a. atricollis*) in southern Africa. *Journal of Zoology* 257: 439–448.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163: 688.
- STUART-FOX, D. M. 2009. A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female-biased sexual size dimorphism. *Evolutionary Ecology* 23: 425–433.
- TILBURY, C. 2010. *Chameleons of Africa: an atlas including the chameleons of Europe, the Middle East and Asia*. Frankfurt, Edition Chimaira/Serpent's Tale NHBD.
- TOLLEY, K., AND M. BURGER. 2007. *Chameleons of southern Africa*. Cape Town, Struik.
- VAN WYK, J., AND K. ELS. 2004. Chamaeleonidae: *Chamaeleo dilepis*: flap-necked Chamaeleon predation. *African Herp News* 37: 21–22.
- VITT, L. J., AND P. A. ZANI. 2005. Ecology and reproduction of *Anolis capito* in rain forest of southeastern Nicaragua. *Journal of Herpetology* 39: 36–42.
- VITT, L. J., P. A. ZANI, J. P. CALDWELL, AND R. D. DURTSCHKE. 1993. Ecology of the whiptail lizard *Cnemidophorus deppii* on a tropical beach. *Canadian Journal of Zoology* 71: 2391–2400.
- WAGER, V. A. 1983. *The Life of the Chameleon. A Wildlife Handbook*. Durban, South Africa, Natal Branch of the Wildlife Society.
- WAPSTRA, E., AND R. SWAIN. 1996. Feeding ecology of the Tasmanian skink, *Niveoscincus ocellatus* (Squamata: Scincidae). *Australian Journal of Zoology* 44: 205–21.
- WHITING, M. J., L. T. REANEY, AND J. S. KEOGH. 2007. Ecology of Wahlberg's velvet gecko, *Homopholis wahlbergii*, in southern Africa. *African Zoology* 42: 38–44.

